NATURAL HISTORY AND GENERAL BEHAVIOR OF THE EPHEMERIDAE NYMPHS HEPTAGENIA INTERPUNCTATA (SAY).

By J. E. Wodsedalek.

There is a comparatively small amount of literature on the behavior of the Ephemeridæ. Probably the best general account is that given in Miall's "Natural History of Aquatic Insects." This treatise contains greatly abridged and reproduced in English, the useful account of the life history of the Ephemera found in Swammerdam's "Biblia Naturæ," and the very entertaining description of Reamur, but the behavior of these insects has been a subject of practically no experimental investigations. The species upon which the present study is based is Heptagenia interpunctata (Say), which is described in Needham's work on "May-Flies and Midges of New York."

HABITAT AND GENERAL HABITS.

Especially in the fall of the year these nymphs are found in ample abundance clinging to the under sides of rocks on the shores of Lake Mendota. Although they may be found under almost any rock, they are most numerous on greenish brown stones corresponding to the coloration of the nymphs, and presenting a rough surface well covered with small aquatic plants. This choice of habitat is probably determined, to a great extent at least, by their negative phototaxis and strong positive thigmotaxis, since I have never seen the nymphs on the upper or the lateral faces of stones.

In a previous paper* the reactions to light and their control by chemicals in H. interpunctata have been discussed in considerable detail. It was found that when the nymphs are placed in a long glass dish of water near a window they immediately swim away from the light. The same negative reaction takes place when the dish is taken into a dark room and a light is introduced near one end. It was also found that this strong negative phototaxis can be reversed by means of various chemical solutions.

*Wodsedalek, J. E. Phototactic Reactions and Their Reversal in the May-Fly Nymphs Heptagenia Interpunctata (Say). Biological Bulletin Volume 21, Pages 265–272, 1911.

The nymphs have a wonderful clinging power. Their flattened bodies, and limbs which extend laterally, are pressed close to the rock, thus enabling the insects to retain their hold and escape the full force of the waves. The legs are supported distally with sharp claws which the nymph digs into the small holes and crevices of the stone. While removing the insects from the stones one can often feel the resistance which they offer despite their small size, and in some cases they cling with such force that their stubbornness often results in the loss of a limb or two. This misfortune however does not seem to be disastrous to the vitality of the insect, and the lost appendages soon regenerate.

Although the nymphs spend most of their time lying quietly, it is astonishing to see with what rapidity they can move with their flattened bodies over the moist surface of stones when they are disturbed, even if the stones are inverted so that the insect is compelled to move with its dorsal surface downward. The latter fashion appears to be even less difficult, owing probably to the fact that they almost continually cling to the under side of rocks in their natural habitat. They frequently move sidewise and even backward, and are so active that an attempt to collect them from stones under water is an almost impossible task.

All summer these insects occupy a narrow strip, about three feet wide, along the lake shore and are particularly numerous on the shores of Picnic Point. Along in the latter part of October as the water turns cool, the nymphs slowly begin to migrate into deeper water and practically all desert the shallow water before the ice begins to form. A careful search was made on the day the ice broke up in the spring but not a single specimen was seen. A few days after the ice disappears, however, the nymphs begin to make their appearance.

I have never seen the nymphs swimming freely in their natural habitat, although when a stone to which several of them are attached is suddenly jerked out of the water, some become dislodged and quickly make for a neighboring rock. They swim in an undulating movement, bending the head, now up, now down, but this locomotion is by no means as rapid as when they are in contact with some object under water. Ordinarily the two lateral setæ are distended at an angle of about forty-five degrees, but during the swimming they are drawn in toward the middle one, thus forming a sort of flexible paddle. When the swimming movements cease, the setæ are again distended, allowing the nymph to sink slowly to the bottom, or to take a short rest in suspension before another seemingly strenuous effort at swimming is resumed. Short distances of two or three inches are usually made with alacrity, but a longer distance seems to fatigue the nymph and little progress is made. However, when shelter is in evidence the movement increases, and almost invariably the nymphs put on extra speed on the home stretch.

May-Fly nymphs obtain their ogyxen from the water by means of the seven pairs of tracheal gills which are attached to the first seven abdominal segments. The nymphs would be quite inconspicuous in their natural habitat were it not for the simultaneous backward and forward motion of the gills. While they are in a quiet attitude, all of the gills are not usually brought into play and their motion varies in proportion to the physical exertion, and to some extent at least, in proportion to the amount of food within the body of the nymph. The motion of the gills can be greatly increased by giving the nymph vigorous exercise and also by keeping it out of water for some time. Specimens destitute of nutrition for several days exercise their gills to a comparatively small degree.

FOOD AND FEEDING.

Ten active specimens were placed in separate dishes of water containing a bare rock, and after a few days of fasting, all chewed at a piece of alga when brought near to their mouth parts, as long as they were attached to a stone, finger, or some other object. It might be well to mention the fact that algæ form the greatest share of the food of these nymphs and that animal food is not taken until the nymphs are well starved, when they chew at almost anything they come in contact with. When the stones were removed, the nymphs refused to eat unless the piece of food was large enough to afford attachment. Some of the nymphs ate almost immediately after coming in contact with the food, while others did not do so until after several days. Others again would attach themselves to smaller pieces of alga, but would not eat unless the particle of food was lightly pressed against their mouth part. Evidently the particle of food was too small to afford comfortable attachment and the soft consistency of the alga did not offer the proper contact stimulus.

There seems to be sufficient evidence that small objects are not seen by the nymphs, for very frequently they will repeatedly ignore a particle of food held in their immediate neighborhood. This is also true of much fatigued specimens which, during their slow search for food, devour the savory morsels only when they accidently hit upon them.

In another experiment I took ten specimens and placed each in a small dish of water containing a carefully measured piece of food. Daily observations were made and the results obtained are tabulated below. The (—) sign indicates that the food remained untouched; the (+) sign is meant to show that part of the food had been eaten, and (O) marks the day when no food remained in the dish:

Specimen	Size of food	1	2	3	4	5	6	7	8	9	10	11	12
1	1 sq.mm.	—	—	—	—	—	—	—	—	O			
2	1.5 "	—	—	—	—	+	—	—	—	di	ed		
3	2 "	—	—	—	—	—	—	—	—	—	O		
4	2.5 "	—	—	—	—	—	—	—	—	—	—	—	O
5	3 "	—	—	—	—	+	—	—	+	O			
6	3.5 "	—	—	+	—	+	+	O					
7	4 "	—	—	—	—	+	+	+	O				
8	4.5 "	—	—	+	+	?	+	O					
9	5 "	—	+	—	—	+	+	+	O				
10	5.5 "	+	+	+	+	+	?	O					

The experiment was repeated with another set of nymphs, and similar results were obtained. Evidently the specimens in the first few cases did not see the piece of food, and ate it only when they came in contact with it by chance.

THIGMOTAXIS.

The strong positive thigmotaxis of the nymphs, as was stated in speaking of their habitat, is apparently the most pronounced feature of their behavior. When several specimens are placed in an aquarium they mass together into clusters where they remain for many hours, and if recently collected, even days. As soon as a rock or any other object is placed in the water, the loose forms swim toward it, while considerable time often elapses before the masses are broken up.

Two long bricks were placed one over the other in a basin of water and between them small pebbles varying in size so that the space gradually varied in thickness from one end to the other. Then a large number of nymphs were put in the water, and after a short time it was found that nearly all of the specimens were attached to the lower surface of the upper brick with their dorsal side downward, and a large majority of the specimens were in that portion of the wedge-shaped space where their backs came in contact with the brick below.

Then a stone to which several nymphs were attached, was placed in a tin pan and the temperature of the water was slowly raised. As the temperature approached 42°C. several specimens began to lose hold of the rock, others clung to it until the temperature reached 45°C. and in no case did the specimens desert the stone until they were completely overcome by the heat. Then a large stone was placed in the pan, half of it being above the surface of the water. On top of this were placed other rocks highly heated and thus heating the stone half submerged, to which the specimens were attached. A piece of ice was kept in the water to keep it cool, while the temperature of the rock was quite high. This time the insects did not hug the rock as tightly as is their natural custom, but clung to it in a sort of half fast fashion. That, however, was not the only sign manifesting discomfort, as upon close observation it was noticed that first one foot would be withdrawn from the hot rock and then another, the specimens clinging by four or five feet at a time and cooling the others. The space between the nymph and the rock would grow wider and wider until the insect would hang by only one or two claws and finally fall down backward to the bottom. As soon as refreshed in the cool water it would again attach itself to the hot rock. This same process was repeated over and over, though when long continued the rock was not sought with such extreme anxiety as in the beginning.

Although most of the nymphs behaved in that way, occasionally one would leave the rock when the temperature of the stone was about 40°C. and would not return for a long time.

When it was brought near the stone again, it would at first swim toward it, but as soon as the heat was felt it would again turn and swim away. Some of the forms, upon coming in contact with the hot rock, would suddenly dart off, make a little circuit, and then return. This was repeated several times, the circuit becoming more and more extended until finally the nymph would no longer return to the stone. Still others would leap from place to place on the rock as though in search of a cool spot, some finally deciding to leave the stone, while others would quietly settle down and like the large majority of them, would cling to the stone until overcome by the heat.

While working on the food reactions, I came across a specimen that showed an exceptionally strong thigmotactic propensity. When it was placed in a separate dish of water it swam about very much animated, and after intervals of rest, its vigorous activity was again resumed. When a stone was placed in the dish the nymph eagerly attached itself and remained perfectly quiet, but when the stone was taken out and a small piece of alga was placed in the dish, the insect would come up to it, attach itself, and then quickly swim away again. The soft consistency of the plant evidently did not appeal to it. The circus movements were repeated every time I appeared near the dish. Not until after five days of fasting did the nymph attach itself to the morsel of food, to which it clung so firmly that its body became a complete ring. Then it commenced to feed on the ball of food it held so tightly in its claws. The smaller the piece of alga became the more tightly the specimen seemed to cling to it. Finally when only a small part of the food was left, the nymph discontinued feeding but still clung to the small particle. Thinking that this was probably due to the chemical stimulus of the plant, I took it away and gave the nymph a tiny pebble about the size of an ordinary sweet pea. The pebble was eagerly accepted but being much too small to afford normal attachment, the nymph coiled itself around the pebble and thus brought as much of its body in contact with it as possible. It continued encircling the pebble for six days when I noticed that it was about to moult. This was a difficult task, and although the pebble was cast aside during the attempt to get out of the old skin, the specimen now retained its ringlike shape. As the nymph was unable to moult in that condition, the old integument was carefully torn off, but the unfortunate specimen still remained helpless, disfigured, and unable to swim. All attempts to make it attach itself to a flat surface were of no avail, as the nymph would spring up like a stretched out hoop and fall to the bottom. When a small pebble was placed against the ventral surface of the insect, it was grasped and held tightly. Every day I gave it a trifle larger pebble and by the time of the next moulting, the nymph almost recovered its normal form.

Undoubtedly the specimen experienced some difficulty from the beginning, in clinging to so small a pebble in such an unnatural condition, and yet the content derived through the contact with the pebble must have been more potent, for the nymph would curl itself about the pebble, getting as much of its body in contact with it as posslble, in spite of the fact that the body coiled itself into a complete ring.

DEATH FEIGNING INSTINCT.

The death feigning instinct is quite pronounced in May-fly nymphs when roughly handled out of water. It is rather difficult, however, to make them feign death in water and when one is successful the feint lasts but a few minutes at the most, usually only a few seconds.* Holmes found that mature Ranatras will feign death very readily when taken out of the water and laid on the table, and that they will endure all sorts of maltreatment during the death-feint, even suffering their legs to be cut off one by one or their bodies cut in two without the least response. Most May-fly nymphs can be made to feign death by taking them out of the water and throwing them on the table, but the time of the feint varies widely in the different individuals, some feigning only a fraction of a minute, and others as long as fifteen minutes. The average death-feint lasts about two or three minutes, but it can be prolonged by stroking the nymph on the sternum or ventral part of the abdomen. Under such conditions some specimens were observed to feign death on a very damp piece of cloth for a period longer than an hour.

By placing nymphs with their backs against a rock, and the abdomen with the tracheal gills submerged under water, I have seen some of them feigning death as long as sixty-five minutes

*Holmes, S. J. Death Feigning in Ranatra. The Journal of Comparative Neurology and Psychology, Volume 16, No. 3, pages 200-216, 1906.

at a time, despite the fact that the anterior part of the body was exposed to the air. I sometimes came across forms that could not be made to feign death at all, in others again, though very rare cases, the feint would be so pronounced that pricking the insects only made them more rigid and apparently under obligation to serve their time in that attitude. Usually, however, a touch with a sharp object makes the nymphs discontinue the feint while a smooth object tends to prolong it. Sometimes, before the recovery from a death-feint, the nymphs begin to move the setæ, or stretch out a limb, and then a quick movement of the other limbs follows. Ordinarily, however, the recovery is a sudden jerk, and occasionally, if the nymph happens to lie ventral side downward, the violent, simultaneous extension of the folded legs throws the nymph into the air. Most nymphs can not be made to feign death longer than fifteen minutes on a dry table, a fact probably due to the disturbance in the metabolism of the body occasioned by the lack of oxygen.

MOULTING AND LIFE CYCLE.

The nymphs moult on the average once in about two weeks; the intervals being largely independent of the age and size of the insect. They grow on the average about one-third of a millimeter during the time which elapses between the two successives moults. They do, however, moult several times after they are apparently full grown, or when the growth in length at least, is not appreciable. The number of moults would probably vary during the different seasons if the nymphs were in their natural out-of-door environment and the almost regular moulting may be possibly influenced by the almost invariable temperature of the water in the aquaria.

Ten individuals varying from one to nine millimeters, were kept in separate dishes with an abundant supply of food; daily observations made, and the dates of the various moults recorded which are given in the following table. Several of the larger forms metamorphosed and some of the small ones died within a month or two, and these I was unable to replace on account of the rare sizes, but two lived as long as the experiment was continued.

I	II	III	IV	V	VI	VII	VIII	IX	X
1 mm.	1.5 mm.	2.5 mm.	3 mm.	4 mm.	5 mm.	6 mm.	7 mm.	8 mm.	9 mm.
Nov. 7	Nov. 8	Nov. 7	Nov. 9	Nov. 8	Nov. 10	Nov. 6	Nov. 8	Nov. 9	Nov. 10
Nov.22	Nov. 20	Nov. 20	Nov. 22	Nov. 20	Nov. 21	Nov. 18	Nov. 18	Nov. 20	Nov. 20
Dec. 3	Dec. 1	Dec. 1	Dec. 4	Dec. 1	Nov. 30	Nov. 30	Nov. 30	Nov. 30	Dec. 1
Dec.19	Dec. 13	Dec. 13	Dec. 15	Dec. 12	Dec. 9	Dec. 8	Dec. 7	Dec. 9	Dec. 12
	Dec. 28	Dec. 23	Dec. 23	Dec. 22	Dec. 22	Dec. 21	Dec. 18	Dec. 19	Dec. 30
	Jan. 13	Jan. 5	Jan. 8	Jan. 4	Jan. 5	Jan. 5	Jan. 4	Jan. 6	Jan. 8
		Jan. 23	Jan. 22	Jan. 15	Jan. 16	Jan. 26	Jan. 20	Jan. 18	Jan. 16
			Feb. 10	Jan. 29	Feb. 2	Feb. 10	Feb. 6	Metamorphosed	Metamorphosed
			Feb. 24	Feb. 12	Feb. 16	Feb. 23	Metamorphosed		
			Mar. 5	Feb. 26	Feb. 28	Metamorphosed			
			Mar. 21	Mar. 4	Mar. 12				
			April 3	Mar. 28	Metamorphosed				
			April 18	April 13					
			May 4	April 29					
			May 19	May 16					
			June 2	May 30					
			June 17	June 16					

Just how long *H. interpunctata* live I am not entirely certain, as I have been unable to keep any specimens throughout their whole life history. However, there seems to be sufficient evidence that their life extends through a period of two years. In the observation on moulting careful measurements were made of all the specimens after each successive moult. From these data the entire life cycle can be inferred. For example, specimen I which was one mm. long November 7, was one and one-half mm. long December 3; specimen II, one and one-half mm. long November 8, was two and one-half mm. long December 13; specimen III, two and one-half mm. long November 7, was three mm. long January 23; specimen IV, November 9, was three mm. long, or the same length as specimen III had attained when its record ceased, was seven mm. long in June.

Specimen VIII which was seven mm. long in November 8, metamorphosed three months later.

Specimen I, which was one of the smallest obtained in November, was apparently an offspring of the last adults of the season, which metamorphosed in the latter part of August. On further plausible supposition, that it hatched the first part of September, specimen I was about three months old on December third, when it was one and one-half mm. long. Adding to this the time it required specimen II to become two and one-half mm. long, and specimen III to attain three mm. and so on, we have a total of nineteen months, an apparent gain of five months. This gain, however, is easily accounted for owing to the fact that the specimens had the advantage of wintering over in the aquaria. Such a gain actually took place in the larger specimens, which metamorphosed in January, February, and March, and no doubt would not have metamorphosed until June, July, or August of the following summer had they remained in their natural habitat.

The members of this species do not all emerge in the same day or few days, as is true in many other Ephemeridæ, but adult specimens may be collected near Lake Mendota any time from the latter part of June to the latter part of August. The emergings are most numerous in the afternoon. The nymphs crawl up on the rocks, a split appears in the median line of the mesothorax which quickly extends through the pro and metathorax. The head appears first and then the thorax, closely followed by the first pair of legs. A few jerks cause the extrication of the wings and a moment later they become erect. The other two pairs of legs are pulled out about the same time and soon the entire subimago is exposed. After a short rest the insect flutters upward and usually settles a short distance away. This whole process is completed within five or six minutes. On several occasions, when the lake was quiet, I observed the entire emerging process take place at the surface of the water. The sub-imago skin is usually shed within a few hours after the emergence, and the entire life of the adult is comparatively short, lasting about six days at the most and many of the specimens live a much shorter time.

I wish to express my thanks to Prof. S. J. Holmes for his suggestions and kind criticisms.

Zoölogical Laboratory, University of Wisconsin.